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THE PRINCIPLE OF THE CONSERVATION OF ENERGY IN BIOLOGICAL EVOLUTION: A RECLAMATION AND CRITIQUE.

BY JOHN A. RYDER.

The present paper owes its existence to the recent discussion of the principle of conservation of energy in relation to biological evolution,[1] at the Rochester meeting of the American Association for the Advancement of Science, August, 1892, and to the fact that I had made a similar criticism[2] of the views of Weismann and his followers nearly two years earlier, which was published in the same journal. My earlier paper, though not as full and complete a refutation of the erroneous opinions of Weismann as Dr. Miles' article, anticipated the latter's main line of argument by almost or quite two years. While this is true, it affords me great pleasure to find that others are coming forward to criticise, from a scientific standpoint, the very vulnerable and untenable position of the Neo-Darwinians. While it is a great satisfaction to be able to hail the advent of new supporters of Lamarck's doctrine, it may be worth while to call the attention of students to the original position of Lamarck, and the ease with which it may be made to conform to the requirements of the doctrine of the conservation of energy as bearing upon organic evolution. In the Introduction to the "Animaux sans Vertèbres" (Ed. of Deshayes and Milne-Edwards, Bruxelles, 1837, Tom. I, p. 14) occur the following statements of principles.

"First Principle: Every fact or phenomenon of which observation makes us cognizant, is essentially physical, and owes its existence or production to some body, or to the relations between bodies."

"Second Principle: Every movement or change, every active force, and every effect whatsoever observed in a body, depend necessarily upon mechanical causes regulated by their laws."

"Third Principle: Every fact or phenomenon observed in a living body is at once a physical fact or phenomenon, and a product of organization."

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[1] Heredity of acquired characters, by Dr. Manly Miles. American Naturalist, XXVI, 1892, pp. 887–900.

[2] A physiological hypothesis of heredity and variation. American Naturalist, January, 1890, pp. 87–92.

Lamarck's laws of metamorphosis or the transmutation of forms, I have rendered as follows from the same source:—

I. "Life, with its peculiar forces, tends to continually augment the volume of all bodies which possess it, and to extend the dimensions of their parts, up to the end of the term of life."

II. "The production of a new organ in an animal body results from a new need which has arisen unexpectedly, and which continues to make itself felt, and which causes new movements to be made to which this need gave origin and maintainance."

III. "The development of the organs and their strength of action are constantly in proportion to the extent or degree to which they are used."

IV. "The fourth law asserts the hereditary transmission of characters acquired under the operation of laws II and III."

The first law tacitly recognizes growth in volume, with its concomitant development of energy, as a factor in evolution, while the second recognizes the fact of physiological or adaptive response. The third supplements the second in a most logical way.

The third law recognizes the quantitative nature of adaptive response in organisms, and has a very wide range of application. It tacitly recognizes what physiologists must now regard as self-evident, namely, that adaptation, so far as that process involves the expenditure of energy, must go on in conformity with the principle of the conservation of energy, a principle which had not been developed as a scientific conception in Lamarck's time.

The "first and second principles," cited above, have some remarkable recent parallels. Lamarck here recognizes the laws of motion, but their connection with the development of energy necessarily escaped him. It is, nevertheless, instructive to cite here Prof. Barker's definition of energy, as given in his recent treatise; "Physics." After some preliminary discussion, Prof. Barker says:—"Energy may be provisionally defined, therefore, as a condition of matter in virtue of which any definite portion of it may be made to effect changes in other definite portions." Now these *changes* referred to by Prof. Barker have to take place through the development of motion, according to mechanical laws. In Lamarck's "third principle," the logical step is taken which leads from the "not living" to the "living" forms of the exhibition of energy. This appreciation, by Lamarck, of the identity of the underlying causes of the physical phenomena of change, and consequently of motion, and the development of energy in living and dead matter, is most remarkable, and indicates that he must have had some sort of inkling or intimation that the energies of living things and dead things were somehow, and in some sense, to be regarded as kindred or mutually convertible, as implied by the modern doctrine of the conservation of force, through a series of intervening anabolic and katabolic steps, as established by modern physiology. Energy is thus stored or rendered potential in form in living bodies by a series of complex chemical processes, in consequence of which motion, or the liberation of energy as heat, nervous energy, muscular motion, is rendered possible.

Lamarck's conceptions were, however, much restricted in application in his own day. They were evidently most clear to him in animal forms, where motions were obvious to the unaided eye. In the study of the microscopic elements, or cells of animals, little had been done in his time. In fact the science of histology had still to be developed, while modern animal and vegetable physiology were still farther removed from him in the future. We can, therefore, be only the more surprised that the prophetic intuitions of Lamarck should have been as far-reaching as they have since proved to be. If, as has been intimated above, we were to grant him the perception of the great principle of the conservation of energy as viewed at the present time, his principles would require but slight modification to conform perfectly to its requirements, as a working hypothesis in the study of the causation of variations.

We are told by the Weismannians, or Neo-Darwinians, that acquired characters, or such as have been developed through use—exercise of function—cannot be inherited. Since all characters whatever could be acquired only through disturbance of the balance or equilibrium of the functions and metabolism during growth, and consequently the relative proportions and normal functional activities of the parts of organisms, the statement that the effects of *use* and *disuse* cannot be inherited, will hardly need refutation at this stage of my argument.

This leads us at once to the essence of the question, namely: Since all characters had to be acquired, it will naturally be asked, "How, then, from a mechanical or physical point of view, were they acquired?"

Weissmann and his followers formulate an hypothesis of the continuity and variability of an immortal isolated germ-plasm, by means of which it is believed that new characters will arise in the course of germ-development, the favorable or useful variants of which in the completely developed organisms, will be preserved by natural selection. The further assumption is also made that no character acquired by the soma, or body of the parent, through use, disuse or mutilation of its parts, can be transmitted to its offspring. The antagonism of Weismann and Lamarck are thus seen to be most perfect.

Weismann, however, has latterly been obliged to admit that it was "absurd to say that an immortal substance can be converted into a mortal substance," as pointed out by Prof. Vines. He has also been compelled, as a consequence, to retreat from his position declaring the immortal molecular stability of germ-plasm. He says: "*An immortal, unalterable living substance does not exist, but only immortal forms of activity as organized matter.*" Upon which Prof. Miles comments as follows: — "The material continuity of the germ plasma is therefore discarded and replaced with the conception of a *mode of motion,* manifest in matter that is continually undergoing metabolic changes."

Weismann is therefore logically driven to entirely abandon his original position. Dr. Miles' answer to Weismann's position regarding mutilations is the only sound argument I have met with in this connection. It is:— "The failure of the effects of injuries or mutilations to make their appearance in the offspring, cannot be admitted as evidence to prove the non-inheritance of acquired characters, as the physiological activities of the system [organization of the species] that are required to produce the morphological peculiarities have not been established, and there can be no tendency of the organism to reproduce them."

It is now proposed to show that Weismann's hypothesis is ultimately forced to assume, or take for granted, the modernized Lamarckian theory of the causes of variation, without acknowledging the appropriation. This is especially true, since he admits the existence of "immortal forms of the activity of organized matter," while rejecting the immortal substance.

Since no mass of matter, living or dead, can change its own configuration, except through the motion of some of its own parts, however small, among themselves, it follows that such a change of configuration signifies the expenditure of energy.

If any body or mass of matter, living or dead, be placed anywhere in space in order that its configuration may be changed, the necessary energy and consequent motion competent to do so must be developed: —

(*a*.) By a physical change in some part of the substance of the mass itself, or,

(*b*.) The necessary energy competent to change the configuration of the mass must be developed in material bodies, external to the mass itself, or,

(*c*.) Part of the energy necessary to produce a change in the configuration of the mass must be developed by a physical change in a portion of the substance of the mass itself, in conjunction or simultaneously with an energy, or energies, developed by a mass or body, masses or bodies, external to itself. These three are the only possible conditions.

But, since all masses, living or dead, at the earth's surface are known to be subject to the action of forces developed within themselves, as well as forces developed external to themselves, the third condition (*c*) holds for all masses living or dead.

Therefore the conclusion is that no mass at the earth's surface, either living or dead, can by any thinkable possibility change its own configuration, except under the condition that a combination of internally and externally developed forces, agencies or energies shall cöoperate to that end. In other words, there can be no change of configuration of a body without the expenditure or dissipation of energy.

Now, for the application of these known principles.

Since variations of configuration, no matter whether they affect the adult organism or its early stages, imply variations in the operation of internally and externally developed forces or energies competent to produce such changes of configuration, it follows that all changes in the forms of organisms involve the expenditure of energy. In other words, all variations in the configuration of organisms must be dynamically caused. This is true for the following reasons: No variation in the configuration, either transient or permanent (and therefore, inheritable) of a living body, can be produced without the cöoperation of internally developed motions, consequently, of energies, with externally developed energies or such as are derived from the external world. Whether these cöoperating energies are measurable or not, it is simply impossible for them not to so cöoperate, since life is characterized by a continuous display of energy. Life is continuous in the material succession and derivation of its individuals, and thus also continuous as to its dynamical or metabolic processes, or the display of its energies. It is safe to say that the continuity of vital energy or the energy of life, is a far more potent agency in the evolution of organic forms, than the continuity and variability of germ plasm, assumed by Weismann. Vital energy and cosmical energy are coexistent and continuously cöoperative. Weismann at last apprehends this.

Therefore, whenever a Weismannian speaks of variations, however he may assume that they are caused, he is forced to tacitly imply that energy is consumed or dissipated in their production, and he is therefore also compelled to tacitly admit the validity of the Lamarckian method of reasoning.

If he tries to escape the snare which has been set for him, as above, he is placed in a still worse and even more compromising position, viz.: the denial of the validity of the universal principle of the conservation of energy.

No character whatever, of any living thing, however trivial, can be acquired without the expenditure of energy and the development of motion in some form; therefore, all characters are so acquired. Consequently, natural selection can choose only from amongst characters such as have been thus dynamically produced, according to Lamarck's original thesis, modified so as to bring it into harmony with the requirements of modern science, or the doctrine of the conservation of energy.

The only way in which a Weismannian, or Neo-Darwinian can now evade the rigorous fatality of the preceding reasoning, is to declare that natural selection includes in the scope of its operations the production of variations. But he is forbidden, and for sound reasons, to do this by the express denial of any such implication or application of natural selection, by the great expounder of that principle, Darwin himself.

Disingenuousness and subterfuge on the part of Weismannians, have hitherto helped to keep the foregoing disagreeable statement of the facts in the background, but the primary fallacy of the Weismannians, or Neo-Darwinians, has now been exposed, and shown to be a sort of biological scare-crow that we may confidently leave to wind, weather and neglect. The mischief that Weismann has done in leading gullible people astray, by most ingeniously throwing sand into their mental eyes, has not been successfully paralleled in recent times. Weismann's views, as shown above, carry with them the implication of the denial of the validity, within the pale. of biology, of the doctrine of the conservation of energy. In that they do this, they must be characterized as unscientific, since they are not in harmony with the spirit of modern science.

So great is the importance of the recognition of the principle of the conservation of energy in the evolution of organic forms, that it is strange that it has not been hitherto declared that it is the very foundation upôn which all further progress in the investigation of biological evolution must proceed.

How this principle is to be applied and extended in biological research, in an experimental way in the future, it is obviously not now possible to indicate in detail, but that such was the method according to which Nature proceeded to evolve new forms, seems to be proven by the fact that organic evolution by superposition has occurred, as is shown by countless facts. If characters have been superposed and intensified in their expression, as is beautifully shown by the evolution of such structures as the nervous system and fœtal membranes, it seems that the interacting energies involved in bringing this about have operated cumulatively. That is, that every gain of surface for better respiration and nutrition, and combinations of both, set the processes of the development of physiological energy going at a greater rate of efficiency, which would accelerate the process of evolution and its morphological possibilities. The rates at which these energies, internally and externally developed, shall interact, cannot be determined by natural selection, but by growth and the motion of parts and particles dependent upon it.

Weïsmann nowhere in his prolix and tedious essays, except in one of the very latest answers to his critics, steps aside to consider energy in relation to the problems he is discussing. He is simply oblivious of the existence of such a thing as energy as affecting the question before him. His facts may or may not have the value he assigns them, his reason often being of the shallowest and most commonplace texture, as for example, when he says: "The object of this process (sexual reproduction) is to create those individual differences which form the material out of which natural selection produces new species." In this case he has mistaken an effect for a cause, and has assigned as the object of sexuality an end or final cause upon which neither he nor any other man can legitimately dogmatize. This absurd view amounts to the same thing as asserting that organisms have the power to develop physiological processes with conscious foresight, so as to avoid harm coming to their race! This is on a par with Balfour's reasoning with respect to the cause or reason of the existence of the polar bodies, namely, as a preventive of parthenogenesis!

The criticisms of E. B. Poulton, in a foot-note on p. 425 of Weismann's Essays, (Eng. Trans.) are similar to those offered long ago by Dr. C. S. Tomes. Poulton, like his predecessor, criticises my views on the mechanical genesis of tooth-forms, without knowing what he is talking about, evidently not having read my paper. He says: "It may be reasonably objected that the most elementary facts concerning the development of teeth, prove that their shapes cannot be altered during the life-time of the individual, except by being worn away." "The shape is predetermined before the tooth has cut the gum." "Hence the Neo-Lamarckian school assumes not the transmission of acquired characters, but the transmission of characters which the parent is unable to acquire!" Anything more unfair or indiscriminating than the above could not be written. I am charged with making statements I never made, and never had the slightest intention of making. As I am the originator of the doctrine of the mechanical genesis of tooth-forms, I will here say in reply that Poulton and Tomes cannot *disprove* that the forms of the crowns of teeth of mammals are *not* altered in shape *in other ways* than by wear, or by means of stresses and consequent permanent strains. If, as I have shown in my original essay, (Proc. Acad. Nat. Sciences, 1878,) crystalline bodies can be permanently bent and strained by persistent stresses, what proof is there to the effect that even hard enamel caps cannot be so altered in the lifetime of the adult? Moreover, I have shown that all the changes of the crown-forms of the molars of the long series of Artiodactyls, have conformed with mechanical exactitude to the requirements of the various degrees of lateral motion of the jaws, and that where these lateral motions were absent, lateral crown-modifications were also absent. In other words, the degree of lateral modification is correlated with the degree of lateral motion, or sweep of the jaws. Later evidence has tended to show that the development of new cusps and roots, in certain cases, takes place at points of maximum wear in certain teeth in the domestic cat, as pointed out to me by my colleague, Prof. Jayne.

This show of logical acumen by my Anglican critic, is useless; the facts are so overwhelmingly against him, as respects the evidence for a mechanical theory of the evolution of the teeth, that there is no other way in which they can be coördinated. This evidence is cumulative in amount and character, and is also an illustration of the cumulative effect of the secular display of a portion of the energy dissipated by a series of organisms, straining even their hard parts into new configurations which have became hereditary, because the soft parts underlying them have been correspondingly modified and moulded by physiologically developed stresses, which have become, so to speak, permanently expressed as physiological strains.[3] As yet there is no proof of the slightest scientific value, that dynamically acquired and thus cumulatively developed characters cannot be inherited, despite all the evidence, mostly worthless, accumulated by Weismann, Poulton and others. For the unfair manner in which the term "acquired character" is used in all sorts of senses, restrictions and limitations by Weismann himself, see a criticism[4] by C. C. Nutting.

In point of fact, every time a new character appears it is self-evident that energy must be expended in order that the necessary movement of parts may be effected; in order that a new form of the organism, or of some part of it, may be assumed. *So far from its being a fact that dynamically acquired characters cannot be inherited, it is an irrefragable fact that dynamically developed characters are the only ones that can be inherited.* How this is accomplished is a matter for further research.

If refuge is sought in a germ-plasm in which capacities for variation are assumed to inhere, it must be assumed that it operates according to a law peculiar to itself, and in defiance of all known external and physical influences, such as modify or control the movements of the constituent particles and masses of all other bodies. Heredity seems to inhere *a la* Weismann in the germ plasm, something after the manner of the inherence of "horologity," or time-keeping properties in a clock, as long ago suggested by Prof. Huxley, when he was exposing the untenable position of the advocates of "vitality," as a kind of energy with no affiliations to other kinds.

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[3] The words "stress" and "strain" are here used by me in the same sense as by engineers and physicists.

[4] American Naturalist, XXVI, 1892, p. 1009.

Prof. Morse's position that the culture experiments of Dr. Dallinger in training monads to withstand gradually increased temperature, until endurance of 158°F. was reached, was an illustration of *natural selection pure and simple,* is also an illustration of the oversight by Neo-Darwinians of the essential energy-factor of the problem.

Since the monad cultures were kept continuously at a gradually rising temperature, there must have been continuous and successive responses in the mechanisms of the protoplasm of the successive generations to the new conditions, else adaptations could not be effected. The failure to apprehend the fact of the continuity of adaptive processes, while the whole burden is thrown upon the discontinuous selective process, is most extraordinary. If none of the monads involved in the earlier stages of the experiment, had undergone certain internal changes owing to the persistence of the new energy-conditions of heat, none would have been modified so as to be selected as the progenitors of a series of generations, capable of sustaining even greater extremes of temperature.

The adaptive process in living forms where energy always is continuously involved, may be fittingly compared to the idea of continuous number, as understood in the calculus, in contrast to discontinuous or integral number in ordinary arithmetic, and typical of the discontinuous process of the selection of integers, or individuals of a race by means of natural selection. This energy-factor cannot be so conveniently ignored, as it is every time the Neo-Darwinians assert that the development of new characters is entirely due to natural selection.

In the paper by the writer, published in 1890, the idea was advanced that heredity itself must be ultimately interpreted in consonance with the doctrine of the conservation of energy. It was then stated that a theory of heredity something like the following would have to be assumed:—

" In the first place, the supposition of a germ-plasma distinct from the plasma of the parent-body is a needless interjection into the machinery of hypothesis of biological evolution. It does not make the matter one whit clearer to suppose that the germ-plasma is necessary, than to suppose that *all of the living plasma of any and every distinct species is an idioplasm, or is specific in so far as that species is concerned.* If we now suppose, as a consequence of the action of the principle of physiological division of labor, first propounded by H. Milne-Edwards, that *all the plasma, or the whole of the specific protoplasm or idioplasm of the organism, becomes physiologically differentiated and incapable of undergoing embryonic development, except that of the germ-cells or germinal plasma,* as long ago urged by Professor Huxley, we get the same result as that reached by Weismann without involving ourselves in the consequences which beset his hypothesis. *This germinal matter is the only functionless and idle plasma in the parent body,* capable of growing and consequently of multiplying its substance within the parental organism at the expense of the surplus metabolism of the latter as a whole. Moreover, the germinal cells are alone capable of detaching themselves, or being detached, from the parental organism as products of over-nutrition, which have become useless to the life of the parent, as assumed in my preliminary paper "On the origin and meaning of sex." This recognizes the apparent fact of the setting aside or isolation of the germ-plasma, but does not make that fact the cause of the stability of species through the continuity of processes of growth, and the assumed but not empirically demonstrated isolation of such germ-plasma. My interpretation is in absolute accord with the requirements of the principles of modern physiology, while the hypothesis of Weismann and his followers is in conflict with those principles, and ultimately, as a necessary consequence, with the still more comprehensive principle of the conservation of energy. Modern physiology, as well as the doctrine of the conservation of energy, positively forbids us to interpose any barrier between the plasma of the parent-body and that of the germ cells, as is done by the promulgators of the hypothesis of the continuity and isolation of the germ-plasma. To do so robs us of the possibility of appealing to the agency of the workings of metabolism as the efficient cause of the modification of the germinal matter. Since metabolism, and all that it implies, is the only agent to which, according to modern physiology, we can appeal, without interjecting gemmules, plastidules, pangens or some other accessory and needless agency into living organisms, as the efficient agents in the transmission of hereditary traits, we are restricted in our choice to metabolism alone. In this way only is it possible to get rid of a *deus ex machina* in the form of an idioplasm in the sense first implied by Nägeli, or of the gemmules of Darwin and Brooks, the plastidules of Haeckel, the pangens of De Vries, or the physiological units of H. Spencer.

"The preceding paragraph contains, in essence, my own hypothesis according to which all the facts of hereditary transmission and variation may be coördinated without losing or rendering unavailable the advantages which may be derived from the supposition that acquired characters may be transmitted.

"In my view metabolism itself becomes the means of transmitting the changes in the adult organism, due to the complex interaction between it and its surroundings to the idle, functionless and passive germ-cells, because it is a demonstrable fact that these are the only cells in a multicellular organism which have no work to perform which is of direct benefit to the individual life of that organism, unless it may be to take up the surplus nutriment not used by the metabolism of the parent-body in the secular exhibition of the sum total of its physiological energies, in the struggle for existence."

According to my view the idioplasmic, or specific molecular character of the plasma of the germ-cells, in common with that of the protoplasm of the whole body (which latter always tends to repair injuries, or even, in lower forms, replace lost parts,) tends, in virtue of its dynamically acquired specific traits, to repeat the organization of its parent type, in the course of its development, not because it is something different from the protoplasm of the cells of the rest of the body, but because it is wholly unspecialized and without other physiological differentiation.

The automatic processes of heredity are an accumulated result of the continuous interaction of internally and externally developed energies during phylogeny. The exact manner in which these have been registered and preserved in germinal cells, or in parts of organisms which have the power to reproduce the whole organism, we cannot yet hope to explain, in that protoplasm itself is a body of such complexity and capability of transformation, that nothing else approaches it, as is proved by the chemistry of its bye-products, the carbon compounds.

We can only suggest that "molecular impressions experienced in the course of variations in the modes of manifestation of, or disturbances of the balance of the metabolism of the parent-body are supposed upon this view to be transmitted as molecular tendencies to the idle or passive plasma of the germ-cells. Variations in the molecular constitution and tendencies of the germinal matter are supposed to thus arise at different times in the same parent, and that, consequently, successive germs may be thus differently impressed. In this way also the molecular tendencies of the plasma of the germ-cells of different individuals may be also modified simultaneously or successively through the effect of enforced changes in the metabolism of multitudes of contemporaneous adult individuals of the same species, thus leading to a tendency toward concurrent or simultaneous variation of offspring in the same or a similar direction.

" It will be seen that this is the only hypothesis which renders the possibility of concurrent or simultaneous variation within the limits of a species either conceivable or intelligible. It also lends itself to an intelligible comprehension of the phenomena of the correlation of the growth of parts, and it is also the only view which holds out any promise of cöordination with the highly ingenious and suggestive hypothesis of Prof. Wilhelm Roux.[5]"

If we now remember that, as development advances, the influence of external disturbing agencies diminishes, so that it is far easier to produce monstrosities or modifications at an early period of development than at a later one, we see that the early steps of ontogenetic processes are far more easily modifiable than the later ones, owing to variations or disturbances of the externally and internally cöoperative energies manifested during growth. We thus add an important qualifying statement to what has preceded, and one that confirms the preceding in a remarkable way, since it serves to prove that the less specialized states of ontogeny are more sensitive to disturbing influences, than the later and more specialized ones.

" It will be at once perceived that my hypothesis of the acquisition of variations and their transmission is the simplest that has yet been offered. It interjects nothing hypothetical into our conception of the physical substratum of living organisms, except the necessarily unknown and unknowable constitution of the molecular factors of metabolism, and thus brought into harmony with the all-inclusive doctrine of the conservation of energy."

Prof. Miles closes his article as follows:—" Questions like these must be answered, to furnish satisfactory explanation of biological activities, and theories of nutrition and heredity in which energy is not recognized as one of the prime factors in every vital process should be received with caution, and the fallacious arguments based upon them estimated at their real value."

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[5] Der Kampf der Theile im Organismus. 8vo., pp. VII, 244, Leipzig, 1891.

Following these observations, my own remarks at the close of my paper of 1890 may be appropriately quoted :—

" In that the doctrine of the isolation of the germ-plasma is in irreconcilable conflict with the great cardinal principle upon which the whole fabric of modern physiological science rears its stately proportions, namely with the general theory of metabolism, and, consequently, with the still more imposing and universal principle of the conservation of energy, we therefore realize what a colossal fabric of speculative rubbish must be consigned to the limbo of untenable and forgotten hypotheses, in what is represented by the misguided labors of the advocates of the existence of an unalterable germ-plasma."